
Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends

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Abstract: Trends in population abundance are often used to monitor species affected by human activities. For highly mobile species in dynamic environments, however, such as cetaceans in the marine realm, natural variability can confound attempts to detect and interpret trends in abundance. Environmental variability can cause dramatic shifts in the distribution of cetaceans, and thus abundance estimates for a fixed region may be based on a different proportion of the population each time. This adds variability, decreasing statistical power to detect trends and introducing uncertainty whether apparent trends represent true changes in population size or merely reflect natural changes in the distribution of cetaceans. To minimize these problems, surveys ideally would be based on species-specific design criteria that optimize sampling within all relevant habitat throughout a species' range. Our knowledge of cetacean habitats is limited, however, and financial and logistic constraints generally force those surveying cetacean abundance to include all species within a limited geographic region. Alternately, it may be possible to account for environmental variability analytically by including models of species-environment patterns in trend analyses, but this will be successful only if such models have interannual predictive power. I developed and evaluated generalized additive models of cetacean sighting rates in relation to environmental variables. I used data from shipboard surveys of Dall's porpoise (*Phocoenoides dalli*) and short-beaked common dolphins (*Delphinus delphis*) conducted in 1991, 1993, and 1996 off California. Sighting rates for these two species are variable and can be partially accounted for by environmental models, but additional surveys are needed to model species-environment relationships adequately. If patterns are consistent across years, generalized additive models may represent an effective tool for reducing uncertainty caused by environmental variability and for improving our ability to detect and interpret trends in abundance.

Modelos Ambientales de Abundancia de Cetáceos: Reducción de la Incertidumbre en Tendencias Poblacionales

Resumen: Las tendencias de la abundancia poblacional son usadas frecuentemente para monitorear especies afectadas por actividades humanas. Sin embargo, para especies altamente móviles en ambientes dinámicos, como los son los cetáceos en el ambiente marino, la variabilidad natural puede confundir nuestra capacidad de detectar e interpretar tendencias de la abundancia. La variabilidad ambiental puede causar sesgos dramáticos en la distribución de los cetáceos, y con ello, las estimaciones de la abundancia para una región pueden basarse en una proporción diferente de la población cada vez que son calculadas. Esto aumenta la variabilidad, disminuyendo el poder estadístico para detectar tendencias, e introduce incertidumbre ya sea porque las aparentes tendencias representan cambios verdaderos en el tamaño poblacional o porque simplemente reflejan cambios naturales en la distribución de los cetáceos. Para minimizar estos problemas, los reconocimientos se deberían basar, idealmente, en criterios de diseño especie-específicos, que optimicen muestreos dentro de todos los hábitats relevantes a lo largo del rango de distribución de las especies. Sin embargo, nuestro conocimiento de los hábitats de los cetáceos es limitado, y las restricciones financieras y logísticas generalmente exigen que los reconocimientos de abundancia de cetáceos incluyan a todas las especies dentro de una región geográfica limitada. Como alternativa, es posible tomar en cuenta toda la variabilidad ambiental analíticamente al incluir modelos de patrones de especies-ambientes en el análisis de tendencias, pero esto solamente puede tener éxito si estos modelos tienen un poder predictivo interanual. He

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desarrollado y evaluado modelos aditivos generalizados de tasas de avistamiento de cetáceos en relación con las variables ambientales. Utilicé datos de reconocimientos desde la borda de barcos de la marsopa de Dall (Phocoenoides dalli) y de delfines comunes de bocico corto (Delphinus delphi) llevados a cabo en 1991, 1993 y 1996 en las costas de California. Las tasas de avistamiento para estas dos especies fueron variables y tomadas en consideración parcialmente por los modelos ambientales; sin embargo, se necesitan reconocimientos adicionales para modelar adecuadamente las relaciones especie-ambiente. Si los patrones son consistentes a través de los años, los modelos aditivos generalizados pueden representar una herramienta efectiva para reducir la incertidumbre causada por la variabilidad ambiental y para mejorar nuestra capacidad para detectar e interpretar tendencias de la abundancia.

Introduction

An important component of managing animal populations is the monitoring of trends in abundance. This approach generally includes estimating abundance (or an index of abundance) at specified time intervals and inferring trends from these measures of abundance via regression methods (Anganuzzi 1993). Measuring abundance can be difficult and imprecise, however, and trend analyses are frequently plagued by low statistical power (Peterman & Bradford 1987; Peterman 1990; Taylor & Gerrodette 1993). Uncertainties in measuring abundance and interpreting trends arise from sampling variability, which can be minimized through proper survey design, and from environmental variability, which is often more difficult to take into account.

Environmental variability can affect population trend analyses in two ways. First, environmental stochasticity—defined as changes in birth and death processes caused by variations in environmental conditions—creates fluctuations in true abundance through time. These fluctuations increase noise and reduce statistical power to detect long-term trends in abundance. The effect of environmental stochasticity is most pronounced in short-lived species with high mortality and growth rates and is less pronounced in long-lived species with high adult survival and low fecundity. Second, changing environmental conditions may affect the geographic distribution of animals. For a fixed survey region that does not include the entire range of a population, this means that a variable proportion of the population will be available for sampling in each year. These *apparent* fluctuations in local abundance also introduce noise and reduce statistical power and may be difficult to separate from true population trends. Migratory species, which may not return to breeding areas each year (i.e., migratory birds, anadromous fishes, and sea turtles), or highly mobile species with large foraging ranges (i.e., marine mammals, predatory marine fishes) are among the most likely to exhibit such a variable survey proportion in different years.

Under the U.S. Marine Mammal Protection Act, cetaceans in U.S. waters are managed on the basis of conservative estimates of abundance and growth rates, com-

bined with past and present information on trends in abundance. Generally, cetacean abundance studies are based on systematic enumeration techniques such as line-transect surveys (Burnham et al. 1980; Buckland et al. 1993) without specific consideration of habitat types, prey availability, or potential large-scale population movement. Due to financial, political, and jurisdictional constraints, the abundance estimates are most often restricted to the U.S. Exclusive Economic Zone or some other fraction of the species' distribution that is deemed appropriate for U.S. management. Most cetaceans found in U.S. waters extend beyond these designated boundaries, however, and the distribution of populations within the survey area can be highly variable. This means that abundance estimates for fixed geographic management regions (e.g., California) may be based on a different proportion of the population in each year (Fig. 1), adding considerable variability to the abundance time series. As a result, power to detect trends is generally low for cetaceans (Gerrodette 1987; Forney et al. 1991; Edwards & Perkins 1992; Taylor & Gerrodette 1993). Even when trends in abundance are detected, their interpretation is problematic because it is difficult to distinguish apparent trends caused by movement from actual trends caused by changes in population size (Anganuzzi et al. 1993; Mangel 1993; Forney 1995).

To reduce the effect of such environmental variability on abundance estimates and trend analyses, cetacean surveys ideally should be based on species-specific design criteria that optimize sampling within all habitat relevant to each species throughout its entire range. In practice, however, species-specific habitats remain largely undefined for most cetaceans, and economic and logistic constraints usually force abundance surveys to be designed broadly for many species within a limited geographic region. Alternately, it may be possible to model the effects of habitat variability analytically, partitioning changes in apparent abundance into components that can and cannot be explained by environmental changes. This would improve trend analyses by reducing unexplained variability. This approach will be successful only if such models have both within-year explanatory power to account for variability in observed abundance patterns and interannual predictive value indicating that the models have cor-

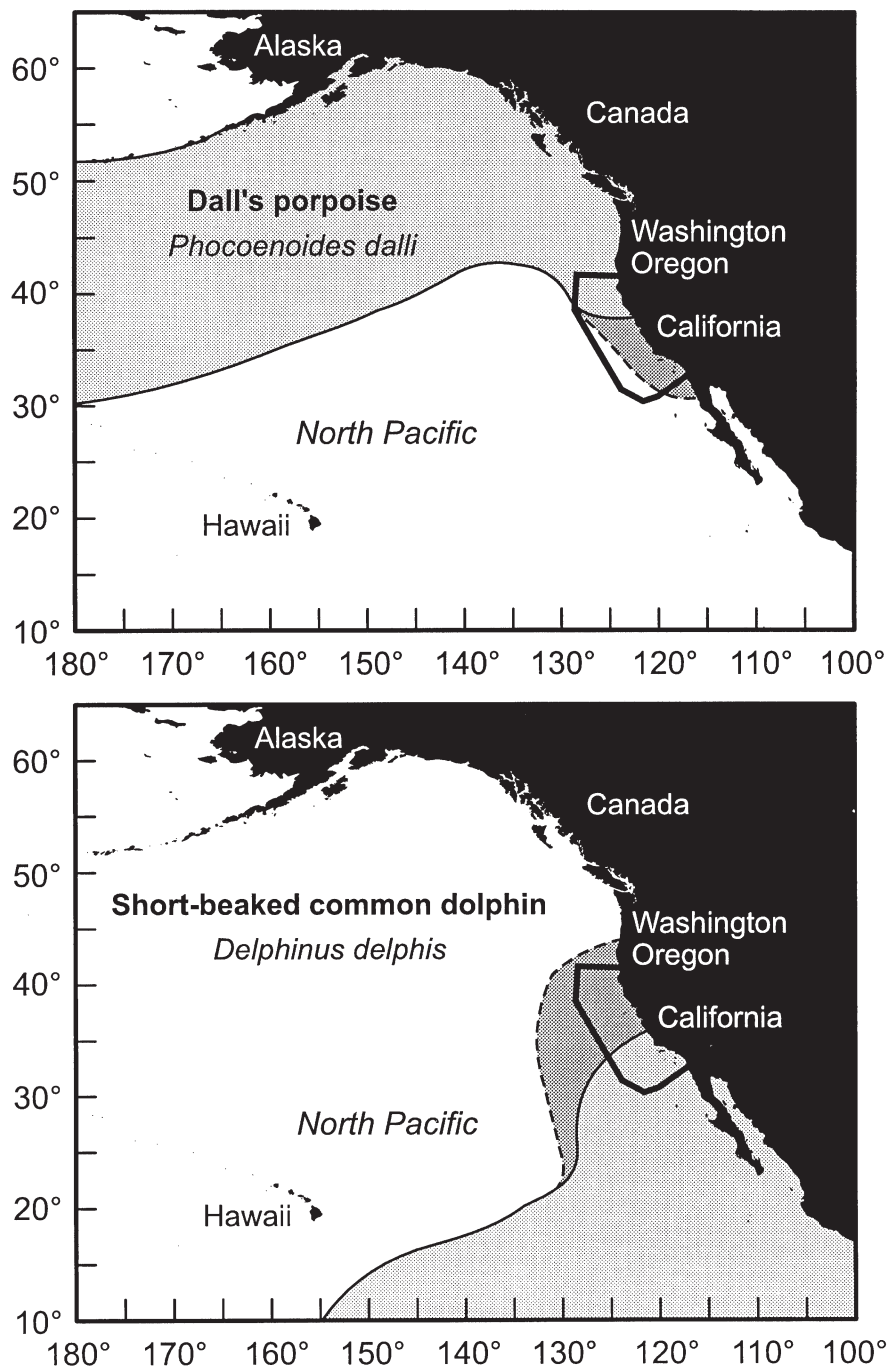


Figure 1. Variation in species distribution for Dall's porpoise and short-beaked common dolphins in the eastern North Pacific Ocean. In different years or seasons, the populations may extend along the California coast to a greater (dark shading, dashed line) or lesser (light shading, thin, solid line) extent. Abundance surveys based on a fixed area, such as the 300 nautical mile survey region in this study (thick line), thus may sample a different proportion of the total population each time.

rectly identified species-environment relationships that are consistent across years. The analytical approach I evaluate involves (1) using environmental data collected simultaneously with cetacean survey data to identify relevant species-environment relationships with nonlinear generalized additive models and (2) testing the ability of such models to predict a measure of cetacean abundance in future years based solely on environmental data. If the predictive value of these models is sufficiently high, they may have merit for improving trend analyses.

The data were derived from shipboard marine mammal surveys conducted within about 555 km of the California coastline in 1991, 1993, and 1996 (Mangels & Gerrodette 1994; Barlow 1995; Barlow 1997). To evaluate the performance of my analytical approach, I investigated as test cases two odontocete species, Dall's porpoise (*Phocoenoides dalli*) and the short-beaked common dolphin (*Delphinus delphis*). These two species are distributed widely (but differently) throughout the eastern North Pacific, with California waters representing only a small portion of their ranges (Fig. 1). Neither species is currently subject to significant

anthropogenic mortality in this region (Barlow et al. 1997), and apparent year-to-year variations in abundance are too large to be caused by population growth processes and therefore must be caused largely by changes in distribution.

Methods

Field Methods

Shipboard line-transect surveys formed the basis of this analysis and are described elsewhere (Hill & Barlow 1992; Mangels & Gerrodette 1994; Barlow 1995; Barlow 1997). Waters within about 555 km (300 nautical miles [nm]) of the California coast (Fig. 2) were surveyed systematically during the summer and fall of 1991, 1993, and 1996 by line-transect methods (Burnham et al. 1980; Buckland et al. 1993). The location and length of transect lines differed among the 3 years, but each survey provided relatively uniform and complete coverage of the study area (Fig. 3). Surveys were conducted aboard the National Oceanic and Atmospheric Administration (NOAA) ship *McArthur* in all

years, and in 1993 and 1996 a second vessel, the NOAA ship *David Starr Jordan*, was also used. The two vessels are similar in size (53 m and 52 m lengths, respectively) and represent comparable survey platforms (Barlow 1997). I used the same field methodology for data collection for all three surveys.

A primary observer team of three observers searched during daylight hours when weather conditions permitted (Beaufort sea states of 0–5 and visibility >1 nm). Two of the observers searched a 90° field of view from the bow to directly abeam of the ship using 25× mounted binoculars. The third observer searched the closer area in front of the vessel by naked eye and with 7× hand-held binoculars. To minimize observer fatigue, all observers rotated through these positions at 30- to 40-minute intervals followed by a 2-hour rest period.

A continuous record of time, geographical position (as determined by a global positioning system), ship's heading and speed, viewing conditions (including sea state, wind speed and direction, sun position, visibility, and presence of rain or fog), and observer identification was maintained on a computer and updated every 40 minutes or when-

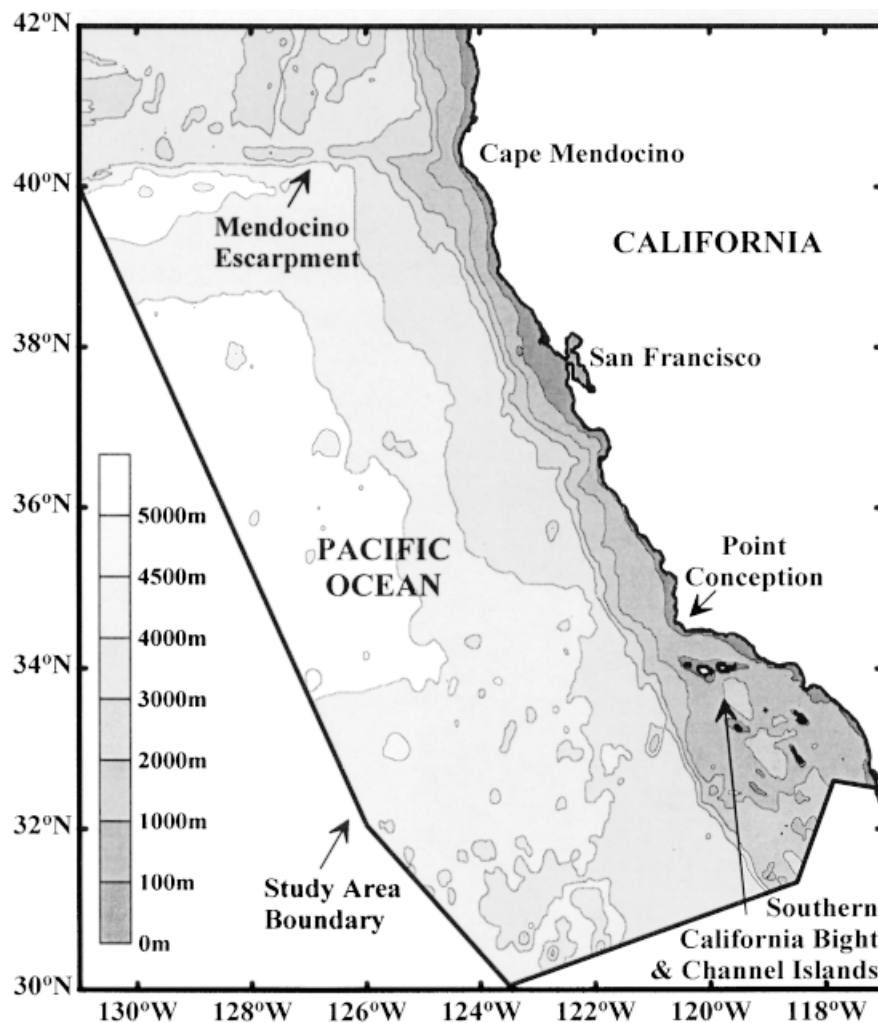


Figure 2. California study-area details, including bathymetric features and landmarks referred to in text. The southern boundary corresponds to the U.S.-Mexican border; the northern boundary is located at the California-Oregon state border.

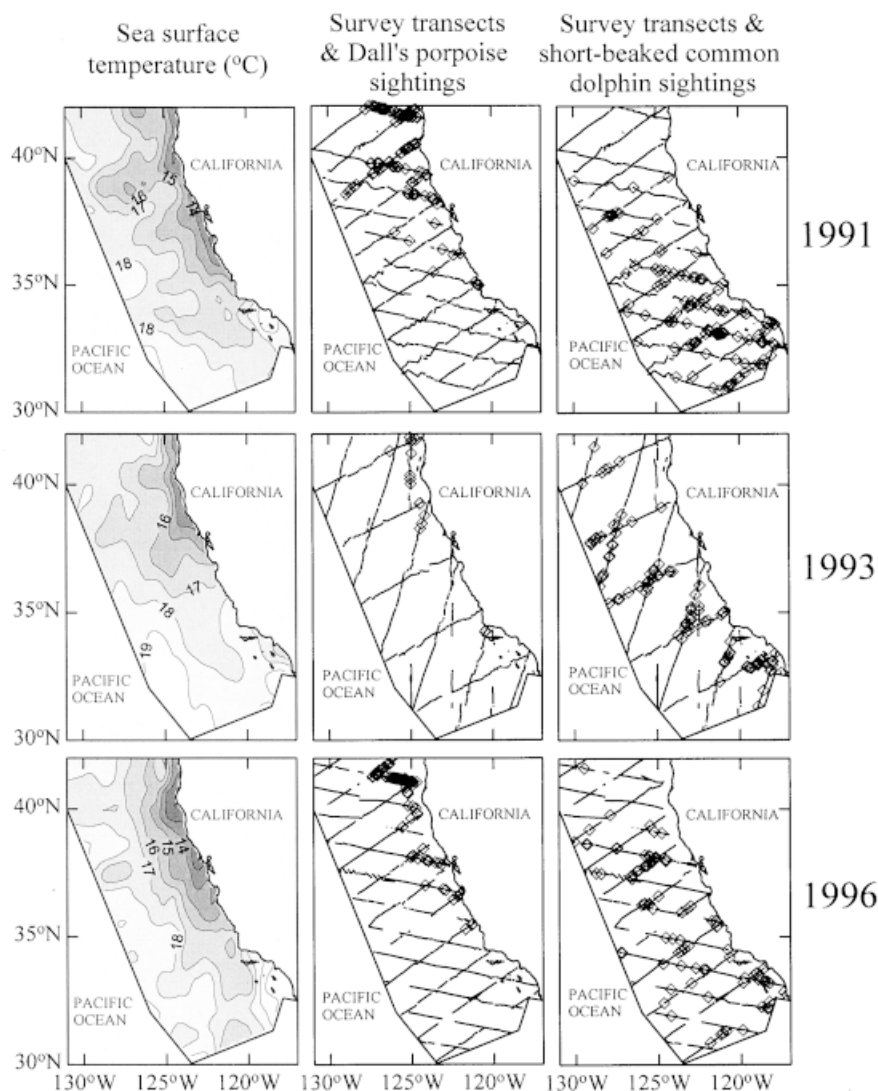


Figure 3. Graphical summary of contoured sea-surface temperature, transect lines surveyed, and sighting locations (◊) for Dall's porpoise and short-beaked common dolphins during 1991, 1993, and 1996 California marine mammal surveys.

ever conditions changed. All marine mammal sightings were recorded systematically, including information on time and position, distance and bearing from the ship, species identification and group composition, and estimated group size. A comprehensive suite of oceanographic data was collected throughout the cruises as conditions permitted (Philbrick et al. 1993). Continuous underway measurements of sea-surface temperature, salinity, and chlorophyll fluorescence were obtained with a thermosalinograph and a fluorometer. Conductivity-temperature-depth (CTD) profiles were obtained each morning before sunrise to allow calibration of the thermosalinograph. I used only the thermosalinograph sea-surface data because processing of the other oceanographic data has not been completed for all three surveys.

Data Manipulations

Marine mammal sighting and effort data for the three surveys were divided into uniform segments for analysis.

Environmental features, such as oceanographic fronts and sea-floor bathymetry, can change rapidly over short distances in California coastal waters, so short segments are required to allow the detection of small-scale patterns. To achieve sufficient resolution, continuous survey transects were cut every 2 km until the end of search effort was reached (e.g., at the end of the day or during bad weather). Any remaining distance at the end of search effort was either included as part of the next segment, if effort resumed at the same location or within about 1 hour travel time, or was excluded from the remainder of the analysis if effort resumed farther away. During all three surveys, most search effort resumed in the vicinity of the previous end-of-effort, and only a small percentage (<0.8%) of the total distance surveyed was excluded in this manner. Each segment was assigned a value representing the number of groups of each target species seen. To maximize sample sizes for modeling, all sightings made during search effort were included regardless of distance from the transect line.

The number of sightings on each 2-km segment ranged from zero to three for both Dall's porpoise and short-beaked common dolphins. These two species were chosen as test cases for this analysis because they had the greatest number of sightings during the 1991 and 1996 surveys and therefore were expected to provide the most robust environmental models.

Based on the available environmental data and past experience with factors that appear to affect marine mammal distribution and abundance, six environmental variables were included in this analysis: (1) Beaufort sea state, which is expected to affect the likelihood of seeing animals rather than true distribution and abundance, included as a ranked categorical variable; (2) water depth, derived from bathymetric data sets that are publically available (NOAA/U.S. National Geophysical Data Center [http://www.ngdc.noaa.gov/mgg/global/seltopo.html] and the California Department of Boating and Waterways through the Scripps Institution of Oceanography Data Zoo [gopher://gopher-ccs.ucsd.edu/11/zoo/bathymetry/cal_boating]); (3) sea-surface temperature based on underway thermosalinograph data; (4) sea-surface salinity based on underway thermosalinograph; (5) latitude; and (6) longitude.

Latitude and longitude were included only as potential interaction effects with sea-surface temperature and depth, as a proxy for different water masses (Reid et al. 1958) and bathymetric regions off California, and to allow the inclusion of potential range-limit effects for both species. Latitude and longitude were not included as main effects in the model because they are not meaningful predictors of cetacean distribution independent of sea-surface temperature and water-depth effects, which are included in the model. Beaufort sea state was usually constant over a scale of 2 km, but if it changed during the course of a segment, the value corresponding to the majority of the segment was assigned. All other environmental variables were evaluated at the midpoints of each segment. Sea-surface temperature and salinity values from the underway thermosalinograph were averaged within 2 km of the midpoint for each segment. Individual water-depth values were estimated from the gridded bathymetric data at the midpoint of each segment by Kriging methods.

Model Development

Models of species sighting rates as a function of a suite of environmental variables were constructed separately from the 1991 and 1996 survey data in the framework of generalized additive models (GAM; Hastie & Tibshirani 1990), a nonparametric extension of the more familiar generalized linear models (GLM; McCullagh & Nelder 1989). In GLMs, the response variable (y) is modeled as a sum of linear relationships with a series of predictor variables (x_1, x_2, \dots, x_n), which may be transformed to produce nonlinear effects according to some specified

parametric function plus a constant, c . A general equation describing this model is

$$y = c + \sum_{i=1}^n \beta_i x_i. \quad (1)$$

Generalized additive models represent a generalization of GLMs. They share many of the same statistical properties but do not constrain the relationship between y and x to be linear or of a particular functional form (e.g., polynomial). In addition to these parametric relationships, GAMs can use smoothing algorithms, such as Lowess or cubic splines, to fit nonparametric functions (Hastie & Tibshirani 1990) to the relationships between y and the x variables. The complete model is the sum of all predictor functions, $f(x)$ plus a constant, c :

$$y = c + \sum_{i=1}^n f(x_i). \quad (2)$$

The advantage of GAMs over GLMs is that they do not require assumptions about the nature of the relationships between predictor and response variables. They can include linear, logarithmic, or polynomial terms (as GLMs do) but also can include a variety of nonlinear relationships that correspond to the patterns actually present in the data, not some prespecified form. For this reason, they are gaining in importance in ecological studies (Cury et al. 1995; Swartzman et al. 1995).

In both GLMs and GAMs, the response can be modeled not only as a normal random process with a mean μ and a variance $\sigma^2 = 1$, but, alternately, non-normally distributed data can be modeled by specification of an appropriate link function between the mean, $E(Y) = \mu$, and the sum of the predictor functions, η (McCullagh & Nelder 1989). For example, a Poisson process can be specified via the log-link function ($\eta = \log(\mu)$) with variance ($V(\mu) = \mu$), and the goodness of fit is measured in terms of the residual deviance rather than the residual error. For Poisson distributions, the residual deviance (D) is calculated as

$$D = \sum r_D^2, \text{ with } r_D = \text{sign}(y - \hat{\mu}) \{ 2 (y \log(y/\hat{\mu}) - y + \hat{\mu}) \}^{1/2}, \quad (3)$$

where y is each observation, $\hat{\mu}$ is the calculated mean, and $\text{sign}(y - \hat{\mu})$ is either plus or minus, depending on the sign of the parenthetical expression (McCullagh & Nelder 1989). Individual Poisson models can be compared by analysis of deviance, which is analogous to the more familiar analysis of variance used for normal distributions.

For this analysis, a generalized additive model was created with the number of sightings per 2-km segment as a Poisson-distributed response variable, and sea state, sea-surface temperature, sea-surface salinity, water depth, and interaction terms involving latitude and longitude as

potential predictor variables. Although they are computationally more intensive than other available smoothers, cubic smoothing splines were used to estimate the functions $f(x)$ because they tend to exhibit superior performance (Hastie & Tibshirani 1990). For each predictor variable, it was first necessary to determine an appropriate level of degrees of freedom (df) to use in the smoothing algorithm. (One df is equivalent to a linear function, and increasing df values allow the function to "track" the actual data points to a greater extent, up to the maximum, where df is equal to the number of data points.) Graphical methods of selecting an appropriate level of smoothing are considered preferable to automatic methods, such as cross-validation, because the latter are less reliable and more expensive to implement (Hastie & Tibshirani 1990). Based on visual inspection of smoothing graphs, a level of smoothing corresponding to 3 df was chosen for all variables in this analysis because it allows nonlinear effects (such as unimodal distributions) and restricts unrealistic detail in the shape of the function. This allows for the detection of major effects but reduces spurious patterns and potential sampling artifacts that can arise from overfitting of the data. The exploratory analyses also revealed that this level of smoothing produced lower values of Akaike's information criterion (AIC; Akaike 1973) than simple linear fits, indicating that nonlinear functions were appropriate.

Model Selection and Evaluation

After selecting the level of smoothing, I constructed models separately for 1991 and 1996 survey data. The 1993 data were not used to construct models because of the lower spatial resolution of the transect grid, the reduced survey effort, and the small number of sightings of Dall's porpoise. Models were selected and evaluated in a three-step process involving (1) a stepwise selection procedure to determine which variables had explanatory power, (2) model selection from the resulting sequence of stepwise models based on predictive power for each of the other 2 survey years, and (3) a cross-validation approach in which the remaining survey year reciprocally served to test predictive power for the other year's best model. First, each variable or interaction term was added to the null model, and the term that resulted in the greatest improvement in model fit was selected for inclusion at the next step. At each successive step, all remaining variables and interactions were again tested individually for possible inclusion. The significance level of each variable or interaction term was evaluated with an analysis of deviance F -ratio test (Chambers & Hastie 1992). These significance levels were used only as a means of evaluating the relative importance of terms in the model; they do not represent absolute probabilities because segments are not independent and therefore the degrees of

freedom in the model are overinflated. My objective was to evaluate the predictive value of such environmental models. No inference regarding the absolute significance of individual terms was intended.

Although the stepwise procedure is used widely for selection of parametric regression models, the greater flexibility of GAMs can result in overfitting the data and adding variables that appear to have within-year explanatory power but which have no interannual predictive power. For this reason, I applied a cross-validation approach to evaluate the accuracy of model predictions for the other 2 survey years. The model step that gave the most accurate predictions for each of the other survey years was selected as the "best model" and then evaluated on the remaining year (done reciprocally for each of the other 2 years). This method provides a mechanism of selecting only those variables that are significant predictors of sighting rates in the year on which the model was based (1991 or 1996) and that also continue to be good predictors in other survey years.

I evaluated the accuracy of predictions by comparing the environmental model predictions to the "null" expectation of the number of sightings, calculated as the product of the 1991 or 1996 encounter rate (number of sightings per kilometer surveyed) and the total number of kilometers surveyed in the other survey year. In the absence of changes in true population size or movement of animals with respect to the study area, this null sighting rate would remain constant among years. The number of sightings predicted by the 1991 and 1996 environmental models for a full survey was calculated as the sum of the expected number of sightings on each survey segment, determined by applying the fitted model to the corresponding predictor variables. The null predictions (based solely on encounter rates) and the environmental model predictions were then compared to the observed number of sightings made in each of the other 2 survey years. A prediction sum of squares was calculated for each model as a measure of performance.

Results

Survey Results

Survey coverage was extensive and approximately uniform during all 3 survey years, with more detailed coverage in 1991 and 1996 than in 1993 (Table 1; Fig. 3). The distribution of effort by viewing conditions (Beaufort sea state) was similar, with about 60% of all effort conducted in Beaufort sea states 3 and 4 in all 3 years (Table 1); in 1996, however, less survey effort was conducted in the best conditions (Beaufort 0–2). The oceanographic environment appears to have differed most notably in the distribution and offshore extent of cold water along the central and northern California coast (Fig. 3). Cold water

was most widespread in 1991, including a long tongue extending southwest from northern California, and least widespread in 1993, when it was confined to a narrower coastal region of northern California. In 1996, sea-surface temperatures were cooler, and contours roughly paralleled the coastline, exhibiting fewer mesoscale features (eddies, filaments) than in the other years. Mean sea-surface temperatures along the surveyed transect lines ranged from 17.0° C to 17.5° C, with a low of 11.0° C and a high of 24.5° C, both in 1996 (Table 1). The warmest mean sea-surface temperature was observed in 1993. Salinities ranged from 30.6 to 33.8 ppm, with mean values of 32.9, 32.8 and 33.0 during the 3 years, respectively. All transect grids covered a similar range of water depths (Fig. 3; Table 1). Sighting rates were variable between years for both species and roughly reflected the patterns of sea-surface temperature. Dall's porpoise, a cold-temperate species, had higher encounter rates in the cooler years of 1991 and 1996 and considerably lower encounter rates in the warmer year 1993 (Table 1). In contrast, short-beaked common dolphins, which are considered a tropical and warm-temperate species, were most frequently sighted during the warmest year, 1993, and least frequently encountered in 1996.

Dall's Porpoise Models

For Dall's porpoise, the 1991-based stepwise selection procedure included (in order of selection) sea-surface temperature (SST), an interaction between SST and latitude, Beaufort sea state, salinity, depth, and an interaction between depth and latitude (Table 2). The 1996-based model included the same variables in a different order of selection (Table 2). The functions were nonlinear for SST, salinity, and Beaufort sea state and approximately linear within the sampled range of depths (Fig. 4).

The 1991 model with the greatest predictive power in 1993 included SST, the interaction between SST and latitude, Beaufort sea state, and salinity; its predicted sighting rate was about 50% closer to the observed sighting rate than the null expectation (Table 2). This model performed third-best in predicting the sighting rates for the 1996 survey. Conversely, the model with the best predictive ability for 1996 (including only SST) estimated a sighting rate similar to both the observed rate and the null expectation and yielded the third-best prediction for 1993 (Table 2).

Overall, the environmental models had a lower prediction error than the null model including only encounter

Table 1. Summary of survey effort, sightings, and environmental conditions during the 1991, 1993, and 1996 shipboard surveys of cetaceans, including Dall's porpoise and short-beaked common dolphin.^a

Units	1991	1993	1996
Survey effort			
Distance surveyed (km)	9998	6250	10360
Beaufort sea state (%)			
0	1.3	0.4	0.1
1	6.4	5.2	5.6
2	14.5	16.8	9.0
3	20.6	30.8	25.7
4	42.7	28.8	34.6
5	14.5	18.0	25.1
Sightings			
Dall's Porpoise			
sightings	94	13	100
sightings/100 km	0.94	0.21	0.97
Common dolphins			
sightings	123	102	97
sightings/100 km	1.23	1.63	0.94
Environment			
Sea-surface temperature (°C)			
range	11.7–20.4	11.3–20.6	11.0–24.5
mean	17.0	17.5	17.2
median	17.3	17.7	17.2
Sea-surface salinity (ppm)			
range	31.7–33.8	30.6–33.5	31.5–34.6
mean	32.9	32.8	33.0
median	32.9	32.8	33.0
Ocean depth (m)			
range ^b	7–4829	9–4810	2–4812
mean	3509	3415	3544
median	4053	3999	3988

^aData include only effort used in the present analysis.

^bMinimum depths are those estimated by the contouring process; actual survey lines did not extend into waters shallower than 18 m.

Table 2. Summary of stepwise selection procedures for Dall's porpoise models based on 1991 and 1996 survey data.

Model year and step	Variables tested ^a	Change in df	Change in deviance	F	Probability	Predicted sighting rate		PRESS ^b
						1993	1996	
1991								
1	SST	2.96	144.36	77.99	<0.0001	0.60	0.91 ^c	0.080 ^c
2	SST × latitude	1.00	101.72	181.94	<0.0001	0.80	0.84	0.181
3	Beaufort sea state	2.98	35.55	30.78	<0.0001	0.58	0.66	0.117
4	salinity	2.99	7.65	7.35	<0.0001	0.56 ^c	0.75	0.086 ^c
5	depth	2.89	3.12	3.14	0.0258	0.61	0.72	0.113
6	depth × latitude	0.78	15.50	63.21	<0.0001	0.64	0.67	0.138
Null (encounter rate) sighting rate						0.94	0.94	0.268
Observed sighting rate						0.21	0.97	
1996						1991	1993	
1	Beaufort sea state	2.92	170.11	39.75	<0.0001	1.31	1.17	0.535
2	depth	2.79	134.06	55.60	<0.0001	0.95 ^c	1.04 ^c	0.345 ^c
3	depth × latitude	0.98	56.30	78.55	<0.0001	1.19	1.15	0.478
4	SST	3.13	24.86	13.85	<0.0001	1.53	1.11	0.578
5	salinity	2.86	10.09	6.23	0.0004	1.49	1.30	0.744
6	SST × latitude	1.04	5.02	8.73	0.0028	1.77	1.42	1.077
Null (encounter rate) sighting rate						0.97	0.97	0.287
Observed sighting rate						0.94	0.21	

^aInteractions are shown with an × between variables; SST is sea surface temperature.

^bPRESS is model prediction sum of squares.

^cBest predictions (those that were closest to the observed sighting rates).

rate information (Table 2). Depth and sea-surface temperature had the most dramatic effects on encounter rates (Fig. 4), with sightings decreasing approximately linearly with depth and dropping off rapidly as SST increased above about 16° C.

The distribution plots (Fig. 3) show that Dall's porpoise off California tend to be seen less frequently in deeper, offshore regions and appear to be tightly linked to regions of cooler water. California represents an approximate southern boundary for this species in the eastern North Pacific (Fig. 1), and it is likely that a smaller proportion of the population extends into California when water temperatures are warmer. The sea-surface temperature × latitude interaction term, which was the second most significant predictor of Dall's porpoise sighting rates for the 1991 model, may also be interpreted in the context of this range limit. Their use of cold-water pockets in the southern part of the study area may depend on conditions farther north, or there may be a time lag before animals reach these areas. The third most significant predictor, Beaufort sea state, affects the likelihood of detecting animals rather than their true distribution and previously has been considered a significant factor affecting sighting rates for this species (Barlow 1995; Turnock et al. 1995).

The 1996 model with the greatest predictive power was the same for both 1991 and 1993 and included only Beaufort sea state and depth. This model gave prediction errors that were somewhat greater than the null model predictions (Table 2). Both models predicted sighting rates close to the observed value in 1991 and substantially overestimated sighting rates for 1993. The poorer

performance of the 1996 model compared to the 1991 model may have been caused by a change in the effect of Beaufort sea state on sighting rates between years. In 1996, higher Beaufort sea states (4–5) had less of a negative effect on sighting rates than in 1991 (Fig. 4), and better conditions appear to have increased sighting rates to a greater extent. Applying the 1996 model of the effects of sea state to other years in which the effects may have differed—due, for example, to changes in personnel or in geographic coverage under varying sea-state conditions—could have resulted in the observed overestimation of expected sighting rates.

Overall, the environmental models for 1991 appear to explain some of the differences in encounter rates between years, whereas the 1996 models do not yield improved predictions over the encounter-rate expectation (Fig. 5). The selection of different model terms in different years (Table 2) suggests that the environmental relationships may have differed between years (such as the ability to detect porpoises in different sea states), that the available variables may not have fully captured the species-environment relationship for Dall's porpoise, or that the model-selection procedure may not have identified the most parsimonious model. Some quantitative differences in the functional relationships between the environmental variables and sighting rates are apparent, but qualitatively, the models constructed for 1991 and 1996 estimated similar functional relationships (Fig. 4). It therefore seems likely that the individual models for 1991 and 1996 each captured some of the same species-environment patterns but that other, within-year differences remained and confounded the overall relation-

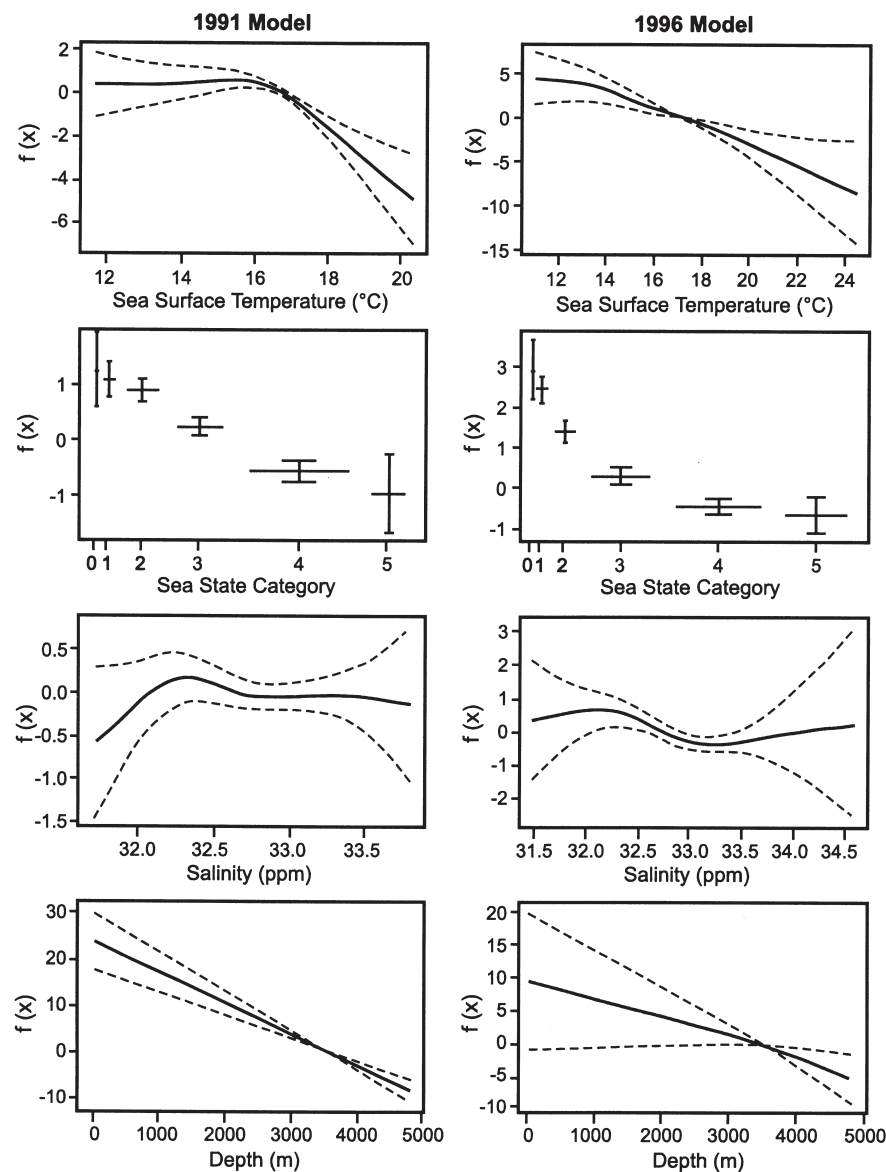


Figure 4. Generalized additive model functions of Dall's porpoise encounter rates in relation to environmental variables for 1991 and 1996 full stepwise models. Functions are scaled relative to the model mean (note different y-axis scales). Sea state, measured on the Beaufort scale, was modeled as an ordered categorical variable, and the width of each function bar represents the sample size. Dashed lines are two standard error bands.

ships, especially for the 1996-based models. Thus, for Dall's porpoise, a single year may not adequately characterize environmental relationships, and additional data will be necessary to build reliable predictive models.

Short-Beaked Common Dolphin Models

For short-beaked common dolphins, the stepwise selection procedure based on 1991 data included sea-surface salinity, sea-surface temperature (SST), and interactions between SST and longitude, and depth and Beaufort sea state (Table 3). The 1996-based model included all the same variables in a different order and an interaction between depth and latitude that was not included in the 1991 model (Table 3). Again, most of the environmental relationships were nonlinear, with the exception of sea-

surface temperature (Fig. 6). For both model years, sighting rates increased dramatically and almost linearly with sea-surface temperature within the range of conditions observed. In 1991, a slight increase in sighting rates occurred at depths below about 3000 m, whereas in 1996 the opposite pattern was found, with sighting rates increasing as depth decreased below 3000 m (Fig. 6). The interaction term between SST and longitude likely reflects the two different sources of warm water along the California coast: the Southern California Bight region (long 117–120°W) shares waters with more tropical regions to the south, whereas warm water at the outer edge of the study area (approximately long 122–130°W) represents the eastern boundary of the central North Pacific gyre. These water masses have different oceanographic properties (Reid et al. 1958), including differences in temperature, nutrients, dissolved oxygen,

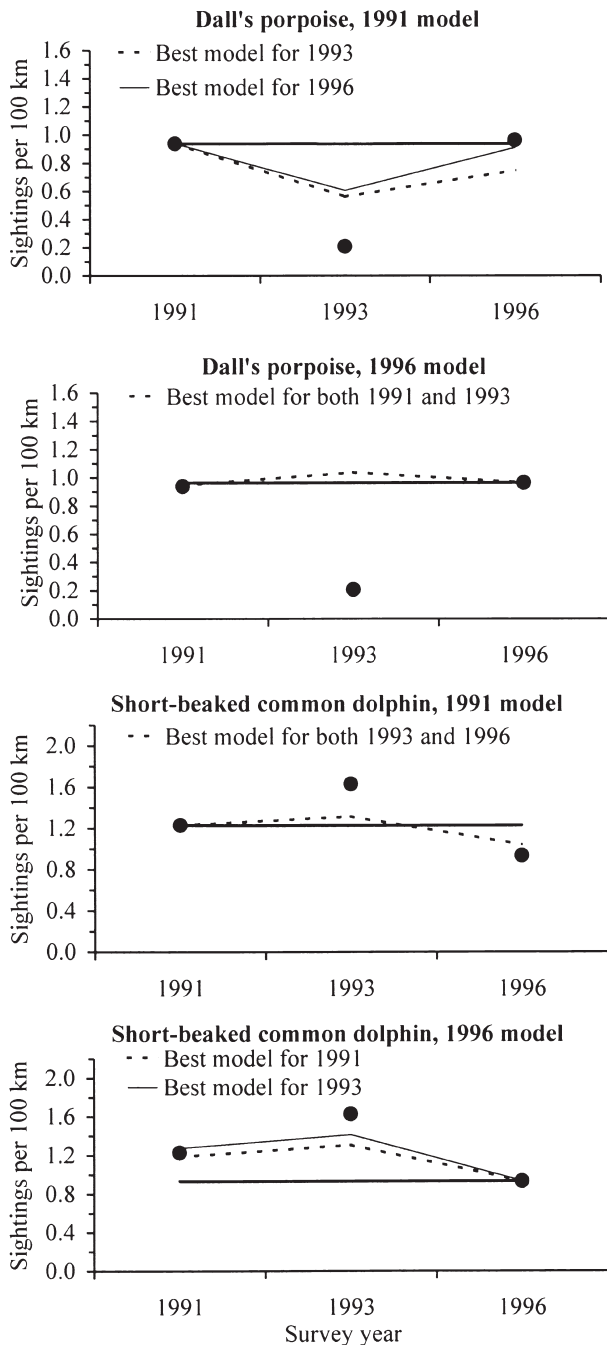


Figure 5. Observed sighting rates (●) and sighting rates predicted by models for Dall's porpoise and short-beaked common dolphins. The null expectation (thick line) represents the encounter rate (number of sightings per 100 km surveyed) for the year on which the models are based (1991 or 1996, respectively). "Best" models are the environmental models that most closely predict the observed sighting rates of the other years. Each best model is applied to environmental data for all 3 years (dashed and thin lines) to evaluate its interannual predictive value. In most cases, predictions for the environmental models are closer to the observed sighting rates than the null expectation.

and salinity. Beaufort sea state, although included in the full stepwise model for both years, was only a component of the "best" models for the 1996 data. This suggests that, as with Dall's porpoise, the effect of sea state may have been different in 1996, but the effect of this difference appears less pronounced for short-beaked common dolphins, probably because they frequently occur in large, active schools and are readily detectable even in higher sea states.

The 1991-based model with the best predictive ability for short-beaked common dolphins was identical for 1993 and 1996, and it included only a subset of the full stepwise model (Table 3). In 1993 the observed sighting rate was higher than any of the model predictions, but the best environmental model prediction was about 23% closer to the observed sighting rate than the null expectation based only on the 1991 encounter rates. For 1996 the best environmental model was about 66% closer to the observed value than the null prediction. Thus, for both years the model predictions were closer to the observed values than the null expectation (Fig. 5), resulting in a smaller prediction sum of squares (Table 3). The observed consistency in model selection between years suggests that the species-environment relationships were reasonably similar in 1993 and 1996, although an unexplained component remains for 1993.

Despite the difference in the order of entry of environmental variables and in the shape of some of the 1991 and 1996 model functions (Fig. 6), the 1996-based models also performed well in terms of their predictions. The best models for 1991 and 1993 differed by only one term, an added interaction between depth and latitude for the best 1993 model (Table 3). In 1991 the best environmental model prediction was close to the observed sighting rate and was about 86% closer to the observed sighting rate than the null expectation (Table 3, Fig. 5). Similarly, for 1993, the best environmental model was about 70% closer to the observed value than the null prediction. Both of these best models had smaller prediction errors (Table 3) than the null model based on encounter rates, and they account for a large proportion of the differences in observed sighting rates for short-beaked common dolphins in 1991 and 1993.

Overall, the environmental models for short-beaked common dolphins seem to have captured more of a consistent pattern between years, and their predictions are considerably better than the null expectation of sighting rates. Some unexplained differences in the shapes of the functional relationships for 1991 and 1996 remain, and it is therefore unlikely that the species-environment relationships have been fully characterized by either of the two single-year models. Despite these limitations, the improved predictive abilities for both 1991- and 1996-based models suggest that this technique is useful for this species even if the relationships have not been perfectly specified. As with Dall's porpoise, it is likely that

Table 3. Summary of stepwise selection procedures for short-beaked common dolphin models based on 1991 and 1996 survey data.

Model year and step	Variables tested ^a	Change in df	Change in deviance	F	Probability	Predicted sighting rate		PRESS ^b
						1993	1996	
1991								
1	salinity	3.00	35.91	11.51	<0.0001	1.13	1.41	0.239
2	SST	2.85	20.08	7.03	0.0001	1.06	1.36	0.255
3	SST × longitude	0.99	30.69	30.23	<0.0001	1.32 ^c	1.04 ^c	0.055 ^c
4	depth	2.96	24.25	8.83	<0.0001	1.13	1.15	0.148
5	Beaufort sea state	2.98	9.08	3.30	0.0197	1.06	1.09	0.178
"Null" (encounter rate) sighting rate						1.23	1.23	0.124
Observed sighting rate						1.63	0.94	
1996								
1	depth	2.96	30.74	8.73	<0.0001	1.04	1.00	0.222
2	Beaufort sea state	2.97	21.07	6.46	0.0002	1.11	1.16	0.120
3	SST	2.96	14.12	4.51	0.0038	1.07	1.12	0.145
4	salinity	2.91	10.39	3.60	0.0138	1.14	1.32	0.054
5	SST × longitude	0.99	11.65	11.61	0.0007	1.28	1.42 ^c	0.024 ^c
6	depth × latitude	0.97	8.26	8.62	0.0037	1.19 ^c	1.31	0.053 ^c
Null (encounter rate) sighting rate						0.94	0.94	0.285
Observed sighting rate						1.23	1.63	

^aInteractions are shown with an × between variables; SST is sea surface temperature.

^bPRESS is model prediction sum of squares.

^cBest predictions (those that were closest to the observed sighting rates)

additional data will allow a more accurate characterization of the relationships.

Discussion

Generalized additive models (GAMs) offer a flexible, nonlinear framework for developing species-environment models without imposing limitations on the form of the underlying relationships. Most of the underlying relationships identified in these analyses were nonlinear, indicating that GAMs are appropriate. For both Dall's porpoise and short-beaked common dolphins, GAMs of sighting rates as a function of environmental variables appear to have some degree of predictive power. This suggests a level of consistency in species-environment patterns for the 3 sampled years, which differed in both oceanographic conditions and observed species densities. If species-environment relationships in future years are similar, such models have the potential to improve our ability to differentiate habitat-related changes in local abundance (due to movement of animals) from true population trends.

The simplest approach would be to use GAMs to include environmental effects when regression analyses are performed on measures of abundance. This type of approach is commonly used to explain nuisance variables in the framework of generalized linear models, and GAMs are an extension of this method, allowing more flexible nonlinear patterns. A generalized additive model of this type has been applied to the interpretation of

trends in harbor porpoise abundance (Forney 1999). Multi-year models only will be valid, however, if the patterns identified are a true reflection of underlying ecological relationships and therefore have interannual predictive power. With additional years, more comprehensive model evaluation may be possible based on the prediction sum of squares as a measure of overall fit. My analysis is intended as a preliminary evaluation of this predictive power for two cetacean species. The results appear promising, but many caveats and analytical complications must be considered when such models are constructed and applied.

The combined stepwise and cross-validation approach to selecting an environmental model was an essential component of this analysis. Preliminary analyses revealed that using only statistical optimization criteria (such as AIC or maximum likelihood) tended to yield models that contained many significant effects, but yet had poor predictive power for other years. This was presumably caused by spurious within-year patterns that did not represent true ecological relationships. Conversely, a simple cross-validation approach based on predictive power alone yielded best models for individual years that contained statistically nonsignificant effects, which were unlikely to have had any underlying biological basis. Ultimately, it is possible that even the more sophisticated three-step model-selection method used in the present analysis may fail to eliminate such "nonsensical" models in all cases. Simulation studies and further evaluation of multiyear models—once additional data are available—will be necessary to confirm or reject the utility of such environmental models in the long term. A multi-year data

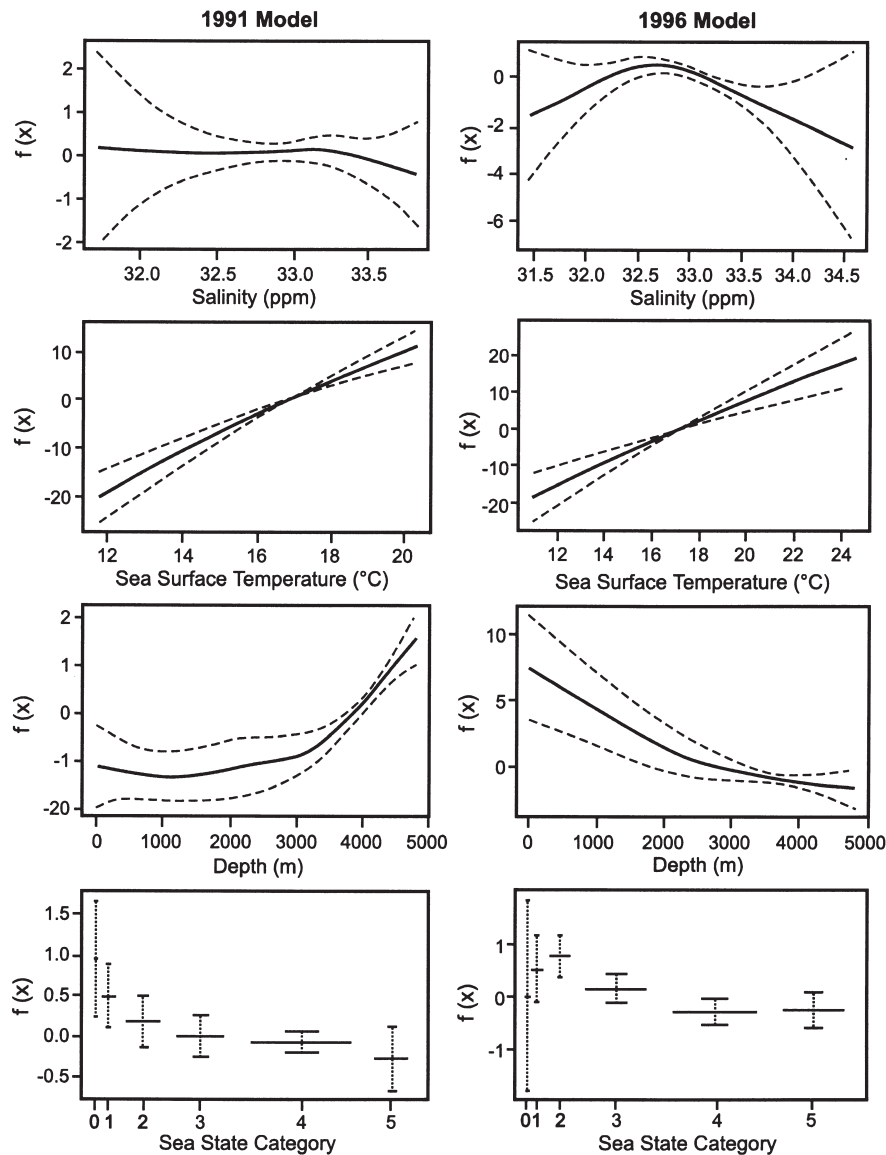


Figure 6. Generalized additive model functions of short-beaked common dolphin encounter rates in relation to environmental variables for 1991 and 1996 full step-wise models. Functions are scaled relative to the model mean (note different y-axes scales). Sea state, measured on the Beaufort scale, was modeled as an ordered categorical variable, and the width of each function bar represents the sample size. Dashed lines are two standard error bands.

set is expected to capture a greater range of observed variability in environmental conditions and their potential effects on the cetacean abundance off California.

As in previous studies of cetacean habitats (Reilly 1990; Fiedler & Reilly 1994; Reilly & Fiedler 1994), unadjusted sighting rates of cetacean schools were used as a measure of abundance in these models. Sighting rates are effectively modeled as a Poisson process, and their use simplified this initial evaluation of environmental models. Other important components of the data, such as school size and distance from the trackline, should ideally be included in future models. The additional complexity introduced with these variables will likely require the development of additional numerical techniques, because Poisson assumptions may no longer be met.

School size was only a minor factor for Dall's porpoise because groups were generally small (1–10 individuals)

and group sizes were relatively constant across the 3 survey years. Mean group sizes were 3.7 (SE 0.4), 4.1 (SE 1.1), and 3.7 (SE 0.4) for 1991, 1993, and 1996, respectively. In contrast, school size may be a confounding factor for common dolphins, which are found in a large range of group sizes (few to thousands of animals), whose mean school size varied between the 3 survey years: 97.3 (SE 8.8), 148.0 (SE 14.6), and 199.0 (SE 19.7) for 1991, 1993, and 1996, respectively. This difference could act to either increase or reduce the remaining unexplained variability, depending on the results of environmental models including a school-size component. For simplicity, distance effects on sighting rates were assumed constant among the years of this study, because the same methodology, vessels, and many of the same observers were used during the three surveys and detection functions were similar (Barlow & Gerrodette 1996; Barlow 1997). Furthermore, the most important factor

affecting detection distance, Beaufort sea state, was included as an explanatory variable, so the models indirectly include at least some distance effects. Presently, it is not possible to include distance modeling explicitly in the models, because sightings are infrequent events and the scale of environmental gradients is only a few kilometers, requiring short segments for analysis.

The two species chosen in this study are taxonomically and ecologically distinct (Jefferson 1988; Evans 1994; Heyning & Perrin 1994), allowing a general evaluation of the developed methodology. It is likely, however, that this approach will work only for species with fairly well-defined habitats. Sample sizes (number of sightings) for most other cetaceans were insufficient in the present data set, and considerably more information will be required before such models can be attempted for rarer species. Furthermore, in some cases, patterns of abundance may be produced by a complex interplay of environmental conditions, and these interactions may not effectively be captured by such models. When selecting environmental variables to measure and include in analyses, it is important to consider what is known about the individual species' ecology and the general oceanographic features of the region under study. Any apparent interactions must be adequately characterized and included in the model-building process.

For example, different water masses and differences in bathymetric complexity were known to exist within the study area (Reid et al. 1958). Bathymetric contours roughly follow a simple north-south axis in central California, whereas the Southern California Bight and Mendocino Escarpment regions contain islands, ridges, and basins, adding topographic complexity (Fig. 2). The water masses found along the California coast differ in oceanographic properties relating to temperature, salinity, nutrients, and dissolved oxygen. In the nearshore regions of central and northern California, higher salinity is generally associated with the colder, nutrient-rich upwelled waters; the southward-flowing, cool, subarctic water has lower salinities (Reid et al. 1958). In nearshore regions off southern California, warm, higher salinity waters coming from the south represent a different water mass than the offshore waters associated with the oligotrophic central North Pacific gyre, which are also warm and saline. Although preliminary analyses revealed no interaction terms between salinity and sea-surface temperature, the resolution of the survey transects may not have been sufficient to resolve this more subtle pattern, and salinity may not be sufficiently reliable for identifying the different water masses (Chelton et al. 1982). For this reason, potential interactions were included (simplistically) as latitude and longitude interaction terms with sea-surface temperature and water depth, based on known oceanographic patterns and on the ecology and distribution of the species. The longitude interaction terms, which were chosen to allow dif-

ferences in bathymetric complexity and water-mass source associated with the southern California Bight to be characterized indirectly, were relevant for the widespread short-beaked common dolphins but not for Dall's porpoise, which were only seen north of this region. Potential interactions with latitude were included for both short-beaked common dolphins and Dall's porpoise because the study area represents their approximate northern and southern range limit, respectively. Without these interaction terms, the models consistently performed worse. It is likely that accurate models will require careful *a priori* consideration and testing of relevant interaction terms.

During all three surveys, additional oceanographic data were collected that will become available in the future, including integrated primary productivity, thermocline depth, sea-surface chlorophyll, average photic zone chlorophyll, surface-water density, and gradients in many of the environmental variables (indicating, for example, regions of steep topography or oceanographic fronts). On future surveys, recent advances in continuous underway sampling of fish eggs (Checkley et al. 1997) may provide a means of directly measuring the availability of some potential prey species. Additional sighting data and environmental variables are expected to improve the characterization of species-environment models.

Overall, the generalized additive models I developed, based on 2 years of data (one for model building and one for model selection), appear to allow improved predictions of expected sighting rates in a third year for two cetacean species; they therefore represent an important step toward reducing unexplained variability in abundance time series and increasing power to detect trends. The results also show, however, that models based on a single year may not adequately capture the nature of individual species-environment relationships. Therefore, models should be constructed with multi-year data and cross-validation methods. Additional cetacean surveys in this region are anticipated at 3- to 5-year intervals, and further analyses are planned once additional data become available. Although this study has focused on problems associated with monitoring long-lived, highly mobile marine species, the analytical techniques evaluated may be applicable to other problems involving non-linear patterns and trend analyses.

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